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Social and Respiratory Behavior of Small Tarpon.

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(Plates I & II; Text-figure 1).

INTRODUCTION.

As part of the program covering a study of the life history and habits of the tarpon, *Tarpon atlanticus* (Cuvier & Valenciennes), a number of small specimens were brought to the laboratories of the New York Aquarium. These were shipped from the field station of that institution on Palmetto Key, Florida, for laboratory study. They had been collected on Sanibel Island by Mr. Marshall Bishop (Breder 1939 a and b).

A consideration of the social attitudes and respiratory behavior of these specimens forms the basis of the present report. These studies have been reinforced by others made in outdoor pools, both in New Jersey and at the Florida field station.

Aside from the actual details which this study works out, the suitability of small tarpon for laboratory work early became apparent. In addition to a most remarkable hardihood, the peculiar specializations of this species lends itself, to a remarkable degree, to a variety of purposes. Some of these will become apparent on a consideration of the body of the report.

For the chemical analysis in Table X by the laboratory of the Bureau of Water Supply of New York City under the direction of Dr. F. E. Hale, we wish to express our thanks. We also wish to thank Mr. R. S. Mathews of the New York Aquarium for assistance during the course of the work.

MATERIALS AND METHODS.

In order to obtain some measure of the attitude of one fish to its fellows, two methods of approach were employed. One consisted of estimating the locomotor behavior of the fishes and the other of estimating the extent of imitation in the specialized respiratory behavior of this species.

The first method, that established by Schuett (1934) and Escobar, Minahan & Shaw (1936) and subsequently used by others, consists of estimating the amount of locomotor activity by noting the travel in a given period of the fish under observation by means of projected cubes from rulings on the glass walls of aquaria.

In these experiments rectangular metal framed aquaria of 50 liters capacity, measuring 60 x 30 x 27 cm. and containing 48 liters, were used. The four sides, which were of transparent glass, were ruled in 8 cm. squares and two mirrors were used to observe movements at the ends. Observation periods of 15 minutes were employed, the distance covered being computed from the number of projected 8 cm. cubes the fish passed through

in that amount of time. The centimeters traversed were obtained by multiplying by 8 the number of cubes traversed.

Each fish was observed for 15 minutes of each hour of a three-hour experimental period. The tarpon used in each day's experiments were selected from a group of ten specimens of the same size, about 10 cm. from the tip of the snout to the base of the tail. In general, experimental tarpon were alternated every day between the various experimental conditions of a particular series so as to distribute evenly any possible daily variations. No observations were made until at least 21 hours had elapsed after a tarpon had been placed in an experimental arrangement. The tarpon were fed chopped herring three times a week at the close of the day's experiments. In general, new water was used at the start of each set of experiments and was not changed during the course of their running. When such water was not oxygenated artificially the oxygen content was 2.0 to 2.7 cc. per liter. When oxygenated it ran from 5.6—5.8 cc. per liter.

Day by day laboratory results for all experiments were checked against the daily barometric pressure readings of the U. S. Weather Bureau, whose New York City station is located one block from the New York Aquarium. No correlations were obtained.

Tarpon respire atmospheric oxygen and for that reason rise to the surface to gulp air at more or less definite intervals. Since this feature might be useful in estimating metabolic activity, such behavior was noted along with the locomotor activity. A marked tendency to rise in groups was evident and this association of fishes in their respiratory movements was likewise studied. Since it is possible to make such studies in the field, observations on the rising of tarpon not confined in small aquaria were also taken for comparison. These field observations on rising tarpon were made in part in a private garden pool of fresh water in northern New Jersey and in part in a pool at the New York Aquarium's Florida field station. The New Jersey pool, of irregular shape, has a surface of 15 square meters and is about 60 cm. deep in its deepest part, and has a volume of 4,300 liters. The water is standing, additions being made only for evaporation, and is for most part crystal clear. The Florida pool is nearly rectangular in outline and has a surface of 115 square meters and is 1 meter deep in its deepest part. The water is standing, supplied only by rain except on the highest spring tides when sea water enters it through a narrow channel. The color is a deep tan. The volume of water is 70,000 liters.

RESULTS OF OBSERVATIONS ON AQUARIUM MATERIAL.

Data obtained in the laboratory, together with their statistical analysis, are given in Tables I to V. Considering only the locomotor portions of these tables, it is evident that under the conditions of these experiments there is little or no significant difference in the locomotor activity between solitary or homotypically grouped tarpon, excepting only some indications of minimal activity in groups of two. This is in contrast to the marked differences found in other species where large differentials have been obtained. Heterotypic groups of tarpon and goldfish indicated a considerable increase in the locomotor activity of the tarpon in association with the normally more active goldfish.

Tables I to V also give the data on aquarium observations of the respiratory efforts. Like the locomotor-activity figures, these show little if any significant relationship between rises for air and various degrees of homotypic grouping. Heterotypic grouping with goldfish shows a general increase in this type of activity paralleling the increased locomotor index.

There appears to be an imitative factor in this rising to the surface for air, as the number of nearly coincidental rises in a group shows a well

marked mathematical significance. Furthermore, it will be shown that models properly manipulated will induce such rises.

Effect of Isolation, Grouping and Tonicity on Locomotor and Respiratory Activity.

Research on the goldfish, a non-schooling form, by Schuett (1934), Escobar, Minahan & Shaw (1936), Breder & Nigrelli (1938) and Shlaifer (1938) has established the fact that goldfishes are significantly more active when isolated than they are when grouped. Tarpon are, like the goldfish, non-schooling forms; however, they are definitely aggregating forms, more so than are goldfish. Accordingly, it was deemed appropriate to observe the behavior of young tarpon in isolation and in groups as regards locomotor activity. Even in well oxygenated water, tarpon rise to the surface periodically to gulp air. They possess alveolar tissue in their lung-like swim-bladder (Babcock, 1936). This pattern of respiratory behavior was employed as an indirect check on metabolic rate and the air-gulp rate (respiratory activity) was noted. Since tarpon live in both fresh and salt water, experiments were performed in both media to determine whether this difference in the chemical environment of the tarpon was reflected in any way in locomotor or respiratory activity.

The statistical analysis of the data in Table I indicates, in general, that there is no significant difference in locomotor and respiratory activity between a tarpon in isolation and in groups either in fresh or salt water and that locomotor and respiratory activity are, in general, the same in both media. There is, however, some indication of minimum locomotor activity in the group of two in fresh water.

Effect of Heterotypic Grouping.

When individual goldfishes were placed in various heterotypic groups of fishes (Shlaifer, 1940), the decreased activity that obtained in homotypic groups disappeared. It was thought desirable to investigate the effect of heterotypic grouping on individual tarpon, although it must be remembered that a tarpon in a group of four has the same rate of locomotor activity as does one in isolation. Tarpon were observed in isolation, in homotypic groups of two and of four and in heterotypic groups containing in one case the experimental tarpon and three orange-colored common goldfishes 10 cm. in length and in the other the experimental tarpon and three golden shiners, *Notemigonus crysoleucas* (Mitchill), colored olive-green and also 10 cm. in length. In the experiments performed on the goldfish heterotypic group and its control homotypic group, the medium was 90% fresh water and 10% sea water and it was not oxygenated, having an average oxygen content of 2.40 cc. per liter. In the experiments performed on the shiner heterotypic group and its control homotypic group, the water was completely fresh, was oxygenated with compressed air and contained 5.62 cc. of oxygen per liter.

The data in Table II again indicate minimum locomotor and respiratory activity in the homotypic group of two tarpon; especially evident, however, is the greatly increased rate of locomotor and respiratory activity in individual tarpon when in the heterotypic situations. At the same time, the data in Table II and Table III indicate that goldfishes and shiners are much more active than are tarpon. Though goldfishes differ markedly in color and to some extent in form from tarpon, shiners do not show nearly such great differences. It is probably, then, merely the disturbing effect of greater activity by the goldfishes and shiners that is responsible for increased activity in the young tarpon. At no time were goldfishes or shiners observed to chase the tarpon and thus directly affect activity. The data also show a distinctly lower rate of respiratory rises when the tarpon are in the highly oxygenated water used in the shiner experiment and its control.

Effect of Visual Contact with the Same and Other Species.

Shlaifer (1939, 1940) demonstrated that the activity of an isolated goldfish was significantly decreased when it was in contact through vision alone with others of its kind as well as when it was actually grouped with them. This line of evidence helped to establish the fact that the group effect was integrated on a visual basis. When goldfishes were grouped with various other species or were in visual contact alone with them, no diminution in activity obtained (Shlaifer, 1940). Since goldfishes and shiners do produce an increase in the activity of individual tarpon grouped with them, it was deemed desirable to pursue the analysis further by eliminating all factors but vision. Table III indicates the results.

Reference to Table III indicates that visual contact alone with goldfishes will also increase significantly the rate of locomotor and respiratory activity of isolated tarpon. In one case, IV vs. IVa, the increase in rises is not significant but from the trend probably would be so with more data. Cross-comparisons between the first parts of Table II and Table III show no significant differences for isolated fishes and those in a group of four in visual contact or grouped together. Though the volume available to the experimental tarpon in the visual contact experiments is only one-half that in Table II, there is no apparent decrease in activity. Amount of available swimming space undoubtedly affects activity in these forms but not between these limits. It will be noted that the activity of the experimental tarpon in actual grouping with three goldfishes is significantly higher than the activity of a tarpon in visual contact alone with these goldfishes. Thus, it may be concluded that while visual contact with goldfishes is enough to increase significantly the activity of isolated tarpon, it is not as effective as when the tarpon is actually grouped with them directly; presumably this is due to the greater chances for disturbing stimuli in the latter case. Additional data in Table III reveal that the goldfishes used in the experiments listed for this table had the same rate of activity as did those in Table II, although the volume available was reduced by half. The goldfishes were, however, significantly more active than the tarpon.

"Imitation" in Respiratory Behavior.

A very interesting pattern of behavior found in the tarpon is the rising to the surface to gulp air by more than one tarpon at a time in a group of two or more. One tarpon will rise to the surface and its rise may be followed immediately by that of one or more other tarpon. This imitative rise does not occur constantly, but apparently, as further data will attempt to show, only when a physiological threshold has been reached. That such imitative rises are truly imitative and not merely coincidental may be determined by the laws of chance. An imitative rise, or at least what we consider to be one, occurs within a second after the initial rise. The minimum time between the rises of any given tarpon that are not imitative is 300 seconds; in other words, tarpon when most active in water not too well oxygenated will rise only once every five minutes. If they are less active and the water is well aerated, the interval is even greater. The data in Table IV were obtained during the running of other experiments.

The data in Table IV indicate that in a group of two, 36.8% of the time a rise by one tarpon will induce a rise by the other. In a group of four, 69.3% of the time a rise by one tarpon will induce a rise in one or more other tarpon in the group. If imitative rises do not occur at random but only when the animal is physiologically ready for an air gulp, then the results are in accordance with expectations. We find in the group of four that the percentage of induction of rises decreases as the number of fishes rising at one time increases. Presumably, the more tarpon, the less the chance that they will all be in a physiologically receptive state for the induction of imitative rises at the same time. However, comparing the group of two with the group of four it is seen that the larger the group the

greater the chance that the rise of one fish will induce an imitative rise in others. Under "additional data" in Table IV may be found evidence for the visual nature of the imitative rise. We find many cases in which the rise of a tarpon on one side of a transparent glass partition in an aquarium will produce imitative rises by tarpon on the other side.

Effect of High Oxygen Content.

Tarpon in nature may be found in salt water that is highly oxygenated and in fresh or brackish water with very low oxygen content. This experiment was designed to investigate the effect of high oxygen content on the locomotor and respiratory activity of tarpon in the laboratory. In previous experiments the water used was not artificially oxygenated and on the average contained 2.0-2.7 cc. of dissolved oxygen per liter. In this experiment compressed air was constantly bubbled through the water and maintained an average oxygen content in the aquaria of 5.81 cc. per liter.

The data in Table V, part A, again indicate no effect of grouping on activity. There is again some indication of minimum activity in the group of two but no significance statistically. When the data for locomotor and respiratory activity are compared with comparable data in Tables I and II, it is seen that while the locomotor activity is the same at the higher oxygen content, the rate of surface rises is significantly less. Thus when the oxygen content of the medium is higher, tarpon apparently utilize more dissolved oxygen and less atmospheric oxygen.

Effective Limits of the Induction of Imitative Rises.

Observations were taken upon individual experimental tarpon in a group of four in order to determine the mean and extreme ranges for non-imitative and imitative rises by the experimental animals and for rises by the non-experimental fishes which did not induce rises in the experimental. Table V, part B, lists the results.

The mean time for an imitative rise by a tarpon, following its previous rise, imitative or non-imitative, is sufficiently close to the mean time for a non-imitative rise to indicate the importance of a physiological respiratory threshold being reached before a rise by one tarpon will induce an imitative one in another. It should be remembered that we consider a rise by a tarpon imitative only if it occurs within a second after a rise by another tarpon in the group. This is not a purely arbitrary assumption, for if the fish does not rise within one second it usually will not rise for a minute or more. The ranges from lowest to highest are great but most data fall close to the mean. It is not easy to explain these extreme ranges. Probably long periods between rises indicate greater oxygen uptake at the last gulp and very short periods indicate very low oxygen uptake. It will be noted from the column titled "mean activity per minute" that at the extreme ranges in the last column the activity per minute (obtained by dividing the centimeters by the number of minutes) does not differ markedly from these means and hence would eliminate the possibility that very low or very high rates of activity were responsible.

Induction of Imitative Rises by a Tarpon Model.

While it is known that the rising of a tarpon to the surface to breathe air may induce an imitative rise in others in a group, it was thought desirable to determine whether such imitative rises could be induced by objects other than the fish themselves. Accordingly, the following experiment was performed:

Four tarpon were placed in water 90% fresh and 10% salt. The average temperature was 21 degrees C. and the average oxygen content 2.69 cc. per liter. Attempts were made to induce rises in the tarpon by periodically

raising to the surface in a typical tarpon respiratory rise a carved wooden model. This model was 10 cm. long, painted silver, and was a reasonably accurate though rough duplication of a tarpon in general body form. It had no fins, eyes nor mouth and was manipulated by the observer by means of two strings tied at its opposite ends.

Many attempts were unsuccessful, as is to be expected if a tarpon does not respond imitatively even to another of its kind unless it has reached a respiratory threshold. However, over a period of 12 hours of observation there were 47 successful inductions of rises in one or more tarpon. The average time for such imitative rises by a tarpon following its last rise was 4.35 minutes. The lowest elapsed time was 1.50 minutes and the highest was 12:00 minutes.

RESULTS OF OBSERVATIONS ON POOL MATERIAL.

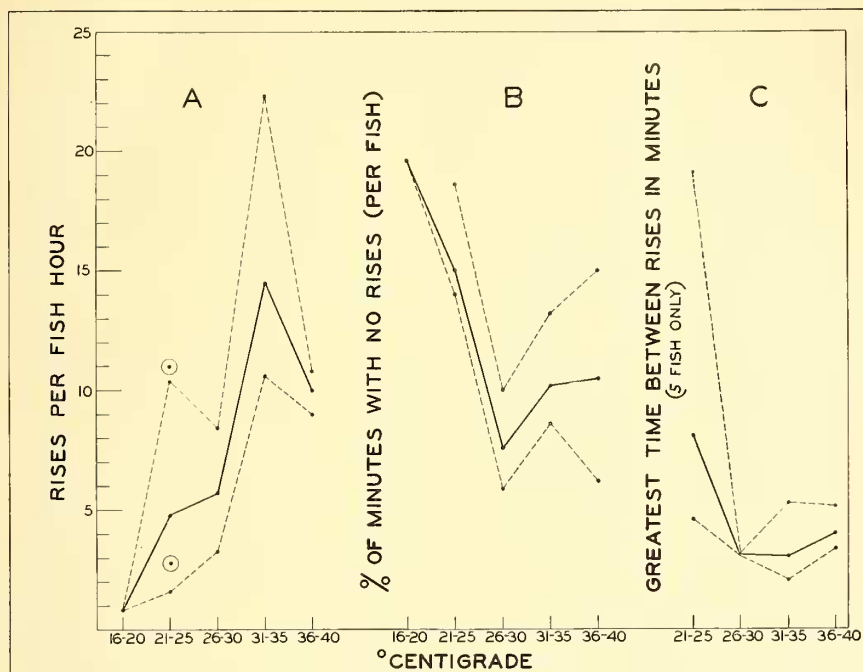
Data obtained in the field, together with analysis, are given in Tables VI to X. Under the conditions, estimates of locomotor activity were impossible, resulting in the confinement of these studies to the respiratory efforts of the tarpon. These fish were mostly of larger size than the aquarium material, the measurements being given in the tables.

"Imitation" in Respiratory Behavior.

The figures obtained on "imitative" rises in the two pools studied are in general agreement with those observed in small aquaria, differing only in the lesser extent of the imitation, Table IX. Since these pools were much larger and the fish able to retreat much further from each other and since the other centrifugal influences of the outdoors were present, this is exactly what should be expected. In accordance with this it is evident that there is a tendency for more fish to rise in groups in closer confinement or larger groups. This, again, would be expected, in that a greater opportunity of seeing a fish rise spontaneously is directly proportional to the number present in a given body of water.

Effect of Temperature on Respiratory Behavior.

In the laboratory the temperature differences were not great enough to give any measurable difference in the number of rises for respiratory purposes relative to thermal differences in the environment. With the large temperature differentials found in the outdoor pools, it was possible to establish a relationship between temperature and the amount of aerial respiratory activity encountered. Table VIII gives the rises per fish per hour tabulated according to the temperature scale in steps of 5 degrees Centigrade. Text-figure 1 illustrates some of the correlations between temperature and various elements in the respiratory rises of these practically wild fish. Table VIII and Graph "A" in this figure show a consistent increase in the number of rises per hour with an increasing temperature, from the lowest temperature to which the fish could be safely subjected without endangering their lives, 16° to 20° C., to a range of 31° to 35° C. Above this, 36° to 40°, which is close to their upper thermal limits, the respiratory rises actually fell off. At this temperature range there was, however, a marked difference in their activity. At the ranges lower than this one they swam about actively, which activity no doubt contributed to their respiratory needs and consistently added to their basic metabolic rate at any given temperature. At this higher level, however, they rested quietly in one place, evidently uncomfortable and making no more effort than was necessary to rise periodically to the surface. This is interpreted to mean that the inhibiting influence on their activity of this high temperature actually reduced their oxygen demand below that at the next lower temperature range where they were normally active.



Text-fig. 1.

Comparison of the respiratory behavior of small tarpon according to temperature in outdoor pools.

The solid line in this chart indicates the mean value as taken from Table VIII while the two dotted lines indicate the maximum and minimum values obtained.

Practical considerations made it impossible to take oxygen readings of the waters of these two pools at the time the observations were made. However, since both were supporting other fishes which are not able to respire air at the same time, they were clearly not near an anaerobic condition. Aquarium experiments in which oxygen content was measured showed that at a content of 2.5 cc. per liter, tarpon rose on the average of 11 times per hour in the 21° to 25° range. This is higher than any reading in the field, where we have good reason to suppose that the oxygen content was at all times considerably above that figure. In similar aquarium experiments at an oxygen content of 5.7 cc. per liter, the same fish rose on an average of 2.8 times per hour. This value is between the mean and minimum of the field observations, and there is reason to suppose that the field conditions more closely approached the latter figure than the former. These two values are indicated on Text-figure 1 by circled dots. It is noteworthy in this connection that the thermally lower parts of this chart were taken in New Jersey and the higher in Florida. Considering the differences in the dissolved salts in these two waters (see Table X), it is rather remarkable that the entire line is so consistent, tending to confirm the aquarium observations with regard to the apparent indifference that these fishes show to the tonicity of their environment.

The field observations were each made for stated periods and tabulated by minutes. Consequently there were always some whole minutes which were represented on the note sheet by blanks. If a similar graph, "B" in Text-figure 1, is plotted showing these minutes without rises, expressed as

percentage of an hour, against a temperature scale, a line is obtained approximately the inverse of that of "A." It is, however, clearly not its mirror image and has the advantage of showing certain features not evident in the former. It, among other things, takes into account the manner of the grouping of the rises and smooths out a simple count of the number in an hour, since it is a measure of arbitrary units (minutes during which the tarpon were "holding their breath." If the imitative efforts of the tarpon modified this need for air seriously, this line should not so closely agree with the first. For example, fish rising a minute or more apart, as compared with all working within one minute in approximate synchronization, would result in vastly different lines. It is notable in this connection that while the number of rises per hour in "A" shows greater consistency (spread between minimum and maximum) in the highest temperature range, in "B" there is a reverse effect, this range showing the greatest spread, indicating that while the fish are probably doing little more than answering physiological needs they are at the same time paying less attention to their fellows.

These data may be handled in still a third way. If the greatest elapsed time between rises in minutes and seconds be plotted against a temperature scale, we obtain a line showing still other tendencies. For practical reasons the figures on this graph are limited to observations concerning five fish. This figure "C" in Text-figure 1 has rather different characteristics and actually the solid line of means is less valuable for consideration than the dotted maximum and minimum, for reasons given below. The line showing the maximum time between rises recorded is a measure of how long the fish can "hold their breath" and actually gives an estimate of the physiological needs of the fish apart from its socialized imitative behavior. The minimum line on the other hand gives an estimation of how soon a fish will follow a fellow to the surface after already having filled his "lung." In other words, this line is more of an index of social attitude than of respiratory need. Thus the mean becomes a time of averages between physiological demand and social influence. It is notable in this connection that the greatest spread between "physiological need" and "sociability" is registered in the lowest temperature range measured. This is interpreted to mean that while tarpon can hold their breath a long time at this temperature, they are also at liberty to be fully social. The line of "maximums" drops sharply with increased temperature, as should be expected from what we have already seen in "A" and "B." The line of "minimums" remains relatively closer to a horizontal line, indicating that their attitude toward their fellows is much less influenced by temperature than is their need for oxygen. It is noteworthy that the time of their greatest sociability is also at the range of their greatest respiratory activity, 31° to 35° C.

A considerable amount of differential behavior was noted in these field observations which is not amenable to statistical treatment.

For example, the pool at the Palmetto Key laboratory showed marked variations in the physical environment from time to time. None of the figures in the calculations show any significant differences associated with these changes, although the observed behavior of the tarpon was distinctly different.

At times when the surface of the water was clear and mirror-like, the fishes generally took their air with a resounding gulp and considerable agitation of the water. The surface disturbance so made is shown in Plate I, Figure 1. The center of the major circle is where the head protruded and the lesser one, to the right, was caused by the tail. This is typical of the rises at such times.

At other times the surface was covered with a scum of green algae that at times formed into a complete blanket. During the processes of formation the rises were much less evident and usually made without any tail splash. Plate I, Figure 2, shows the conditions during the formation of

such an algal scum. A fish had just risen to the left of center. This represents about the maximum disturbance under such conditions.

Later when the scum completely covered the pool, the disturbance incident to rises was even less. The algal blanket was such that it entrained and held the exhaled air, which floated on the surface for some minutes as bright green bubbles. This condition is shown in Plate I, Figure 3. The various bubbles are almost entirely from tarpon exhalations. As the fish normally emit a bubble from each gill opening, these were frequently seen as paired bubbles. The two largest to the left of center are such a pair, from the most recent rise.

While some of these features are referable to the physical condition of the water, the impression was gained that the tarpon disliked coming in contact with the green scum any more than was necessary, avoiding the usual tarpon "roll" of clear water.

DISCUSSION.

Since differences in the locomotor behavior of fishes may be used as one kind of measure of their mental state or psychic attitude toward their fellows, the recent development of a simple method of estimating these differences has stimulated work along such lines. Up to the present all species used for this type of study have shown distinct differences in the amount of locomotion in association with various groupings, homotypic or heterotypic. The species used have been *Carassius auratus*, Schuett (1934), Escobar, Minahan & Shaw (1936), Shlaifer (1938, 1939, 1940) Breder & Nigrelli (1938); *Gambusia affinis*, Escobar, Minahan & Shaw (1936). All considered the extent of travel per unit of time. In addition, Breder & Nigrelli (1938) considered the configurational pattern in three dimensional space and found similar differentiable behavior.

With this as a background, it came somewhat as a surprise to find that the tarpon, a markedly aggregating form, gave no mathematically significant figures from its locomotor behavior when alone or in aggregations. If such is present, it is extremely feeble as compared with the species previously studied, as all studies have been based on a reasonably comparable amount of data. It thus appears that this method may or may not be useful merely on a basis of whether it "works." Evidently fishes are no more uniform from group to group in this regard than they are in others.

This, obviously, is not to say that tarpon are indifferent to one another, for even a most superficial examination will show their strong aggregating tendency. Very possibly the difficulty lies in their relative inactivity as compared, for example, to the goldfish or shiners. When in the presence of the latter they show a marked increase in travel. That this relative inactivity is not merely a condition imposed by close confinement is evident when it is considered that in the garden pool of clear water their behavior was closely similar to that of the small aquaria; *i.e.*, at nearly all times they were quietly aggregated in a relatively compact group, spaced about as they were in the aquarium.

That the metabolic rate is not vastly different under various conditions of grouping is shown by the similarity of their rising to breathe under different groupings; it rises notably only in the presence of goldfish, which no doubt is a result of their greater muscular exertions incident to their increased activity in swimming. Thus we are obliged to leave this portion of the study with the conclusion that the method of estimating social attitude from a basis of locomotor activity is not useful in estimating the social attitude of tarpon, on a purely pragmatic basis.

Since tarpon will rise to breathe air for purely physiological reasons and will also imitate each other in this item of behavior, there are thus two elements involved. While the full separation of them would be exceed-

ingly difficult, it has been shown in the tables that there is a high degree of imitation involved.

Very low oxygen concentrations induce more rises per hour, as would be expected, but grouping and changes in volume seem to have little effect. An unknown variable that must be considered in this connection is the amount of air exchanged on any given gulp. Judging from the figures, however, this would seem to have scant bearing on the social part of this behavior. The work of Schlaifer (1939) on the oxygen consumption of the goldfish, in which he showed that the rate varied with the grouping, could only be used in the present species in a properly arranged metabolic chamber, since both aerial and aquatic respiration are involved. As evidenced by the social factors to be seen in the rising behavior, such a study should be expected to give similar results.

In all these observations a rise has been considered imitative only if made a second or less after the initial rise. Those of a larger time interval have been considered independent. The question arises as to how long such behavior can be considered imitative, or, in other words, what of the memory image and inhibiting influences that give delayed responses? It would seem that first the tarpon must be in a physiologically receptive state, *i.e.*, have not recently gulped air, for two gulps in rapid succession have never been noted. Thus, if a tarpon has partly used up its air supply it may respond with more or less immediateness on the sight of an individual rising to breathe in response to a purely physiological need.

SUMMARY.

1. The locomotor behavior of tarpon is not a useful index in estimating their homotypic group behavior, nor is the extent of their rising to the surface to breathe.
2. There is a marked tendency toward imitation in tarpon rising to breathe, which is of social rather than physiological significance. More or less crude models properly manipulated will induce rises to breathe.
3. Observations in the field, checked against those in small aquaria, agree as to respiratory behavior and indicate the validity of the use of small aquaria for such purposes.
4. Goldfish and shiners, which are more active, induce in tarpon a marked increase in both locomotor and respiratory activity, as do goldfish with which tarpon are in contact through vision alone.
5. Environmental changes including barometric, chemical (salt and fresh water) and capacity of aquaria, do not significantly change the locomotor or respiratory behavior of tarpon, but a large reduction in dissolved oxygen increases respiratory activity. Large temperature changes also result in the alteration of the respiratory activity.

TABLE I.
Effect of Grouping on the Locomotor and Respiratory Activity of Small Tarpon.

Exp. Cond.	I. In Isolation			II. In Group of Two			IV. In Group of Four		
	Mean Activity ³	Mean No. of Rises ⁴	Cm. per Rise	Mean Activity ³	Mean No. of Rises ⁴	Cm. per Rise	Mean Activity ³	Mean No. of Rises ⁴	Cm. per Rise
A ¹	480.0	2.9	165.5	524.0	2.8	187.1	433.6	2.5	173.4
B ²	418.4	2.6	160.9	312.0	2.3	135.6	473.6	3.0	157.8

Exp. Cond.	Statistical Analysis in P-Values ⁵ .					
	I vs. II	I vs. IV	II vs. IV	I A ⁶ vs. I B	II A vs. II B	IV A vs. IV B
A	0.5570	0.4589	0.4823	0.0908	0.5525	0.5444
B	0.1292	0.5570	0.4765	0.4940	0.0100	0.1631

¹ Volume is 48 liters of sea water in a 50-liter aquarium.

² Volume is 48 liters of water, 90% fresh, 10% salt, in a 50-liter aquarium.

³ Expressed in centimeters traversed per fish per 15-minute period of observation. In this and subsequent tables all figures listed under *mean activity* and *mean number of rises* refer to the average for each individual in the particular experimental condition and in each group forty-eight 15-minute periods of observation were divided equally among the number of fishes present when these were tarpon grouped together.

⁴ Expressed in surface rises to gulp air per fish per 15-minute period of observation.

⁵ Upper limit of statistical significance is set at 0.05. This is three times the probable error. P = 0.01 indicates good significance, while a value of 0.100 or more indicates little significance.

⁶ Letter refers to the experimental condition.

⁷ Indicates no significance calculated, since means are almost identical.

TABLE II.
Effect of Isolation, Homotypic and Heterotypic Grouping on the Locomotor and Respiratory Activity of Small Tarpon¹.

Part A—Goldfish.				Part B—Shiners.			
I. In Isolation		II. In Homotypic Group of Two		IV. In Homotypic Group of Four		IVa. In Heterotypic Group of Four ²	
Mean No. of Rises ³	Cm. per Rise	Mean No. of Rises ⁴	Cm. per Rise	Mean No. of Rises ⁴	Cm. per Rise	Mean No. of Rises ³	Cm. per Rise
496.0	2.1	221.6	236.1	586.4	217.1	1753.6	254.1
Statistical Analysis in P-Values.							
I vs. II		I vs. IV		II vs. IV		IV vs. IVa	
Activity	Rises	Activity	Rises	Activity	Rises	Activity	Rises
0.0002	0.0036	0.1900	0.2476	0.0000	0.0000	0.0000	0.0000
Part B—Shiners.							
V. In Homotypic Group ⁶		Va. In Heterotypic Group ⁷		Mean Activity of Non-test Tarpon in Homotypic Group ⁸		Mean Activity of Non-test Shiners in Heterotypic Group ⁸	
Exp. Cond. ⁵	Mean No. of Rises ⁹	Mean No. of Rises	Cm. per Rise	Mean No. of Rises	Cm. per Rise	470.4	3360.2
A	289.6	0.6	816.0	1.1	853.1		

Statistical Significances.
V vs. Va—Activity—.0134
V vs. Va—Rises—.0374
Non-test Tarpon vs. Non-test Shiners—Activity—0.0000

¹ Volume is 48 liters of water, 90% fresh and 10% salt, in a 50-liter aquarium.
² Consists of experimental tarpon and three goldfish, *Carassius auratus* (Linnaeus).
³ See Footnote No. 3 of Table I.
⁴ Expressed in surface rises to gulp air per fish per 15-minute period of observation.
⁵ Volume is 48 liters of water, 100% fresh, in a 50-liter aquarium. Temperature is 74 degrees F. Average oxygen content—5.62 cc. per liter.
⁶ Experimental tarpon is grouped with three other tarpon.
⁷ Experimental tarpon is grouped with three golden shiners, *Notemigonus crysoleucas* (Mitchill).
⁸ Expressed in centimeters traversed per fish per 15-minute period of observation. Figure given is the mean of forty-eight 15-minute periods.
⁹ Expressed in surface rises to gulp air per fish per 15-minute period of observation. Figure given is the mean of forty-eight 15-minute periods.

TABLE IV.
Degree of Imitation in Respiratory Activity¹.

Fish Rises	A ²		B ³		C ⁴		A, B and C combined		%
	In Group of Two	No. of Rises	In Group of Two	No. of Rises	In Group of Two	No. of Rises	In Group of Two	No. of Rises	
Alone		40		40		66		146	63.2
With one Companion		48		15		22		85	36.8
Alone	In Group of Four	38	In Group of Four	13	In Group of Four	52	In Group of Four	103	30.7
With one Companion		37		21		39		97	29.0
With two Companions		31		9		44		84	25.1
With three Companions		11		1		39		51	15.2

Additional data.

Of 177 rises of isolated tarpon in IV of Table III, 23 were induced by the rises of the three tarpon with which it was in visual contact.

In 23 instances out of 218, the rises of the isolated tarpon in IV of Table III induced rises in the tarpon with which it was in visual contact.

¹ All observations taken on homotypic groups of tarpon.

² Data based on observations taken during the running of A of Table I.

³ Data based on observations taken during the running of B of Table I.

⁴ Data based on observations taken during the running of the experiments of Table IIA.

TABLE VI.

Respiratory Activity in a Fresh-Water Pool in New Jersey¹.
(One-half Hour Observation Periods).

No. of rises of all fish to surface in groups of:

Date	Time	°C	No. Fish									Total	
			1	2	3	4	5	6	7	8	9		
6/8 ²	1:28	24	5	3	6	6	0	0	—	—	—	—	15
6/8 ²	2:04	24	5	6	10	6	4	0	—	—	—	—	26
6/9 ³	11:00	24	5	1	0	3	0	0	—	—	—	—	4
6/9 ³	11:45	24	5	5	0	0	0	0	—	—	—	—	5
6/9 ⁴	3:40	23	5	8	4	3	0	0	—	—	—	—	15
6/9 ⁴	4:16	23	5	3	2	3	0	0	—	—	—	—	8
7/14 ⁵	11:21	21	5	13	0	0	0	0	—	—	—	—	13
7/14 ⁵	11:51	21	5	10	0	0	0	0	—	—	—	—	10
7/20 ⁶	2:35	26	9	11	4	0	0	0	0	0	0	0	15
7/20 ⁶	3:05	26	9	16	4	3	0	0	0	0	0	0	23
8/25 ⁷	11:00	18	5	0	2	0	0	0	—	—	—	—	2

Calculations.

Rises per fish hour	Fish rising in groups by percent of total:									All	Per fish
	1	2	3	4	5	6	7	8	9		
6.0	20	40	40	00	00	—	—	—	—	73	14.6
10.4	24	37	24	15	00	—	—	—	—	57	11.4
1.6	25	00	75	00	00	—	—	—	—	93	18.6
2.0	100	00	00	00	00	—	—	—	—	83	16.6
6.0	54	26	20	00	00	—	—	—	—	73	14.6
3.2	38	25	37	00	00	—	—	—	—	83	16.6
5.2	100	00	00	00	00	—	—	—	—	70	14.0
4.0	100	00	00	00	00	—	—	—	—	70	14.0
3.3	73	27	00	00	00	00	00	00	00	63	7.0
5.1	70	17	13	00	00	00	00	00	00	53	5.9
0.8	00	100	00	00	00	—	—	—	—	98	19.6

¹ Fish used in this experiment: 9.5, 12.5, 11.25, 10.25, 10.75 cm. in standard length, placed in pool June 7. Added July 19: 11.1, 10.0, 11.9 cm. in standard length. This pool, recently made of concrete, is fed from a pipeline running from a private home. Water lillies and some *Lebistes reticulatus*, together with an occasional volunteer *Rana catesbiana*, make up the remaining fauna.

² Fish remaining in deepest part of pool in a small aggregation. Partly cloudy with a slight haze; light s-w breeze. Rain threatening.

³ Fair with light easterly breeze. Rain had fallen from 7:00 to 10:00 a.m.

⁴ Thunder with rain threatening. Hazy and overcast. A small trickle of fresh water entering pool. Rain began at 4:35 p.m.

⁵ Sun bright, water crystal clear. Fish active, swimming in a larger group than before, over an area of about 4 ft. in diameter.

⁶ Humid and partly overcast; hazy. Light drizzle at 2:40 p.m. Fish in n-w corner, rising very quietly. Fish near surface for most part.

⁷ Cloudy, chilly. Weather has been unseasonably cold for some time.

⁸ Based on initial data, not shown in first part of table.

TABLE VII.

Respiratory Activity in a Brackish Water Pool in Florida¹.
(One Hour Observation Periods).

Date	Time	°C	No. fish	Number of rises of all fish in groups of:					Total
				1	2	3	4	5	
6/23 ²	9:27	33.5	5	31	22	15	8	5	81
6/25 ³	9:42	30.5	5	29	8	6	0	0	43
6/26 ⁴	9:52	33.0	5	25	16	12	0	0	53
6/26 ⁵	4:52	36.5	5	25	16	12	0	0	53
6/29 ⁶	9:34	34.0	5	50	16	3	0	5	74
6/29 ⁷	3:31	39.0	5	34	6	3	4	0	47
6/30 ⁸	11:58	37.0	5	20	18	12	4	0	54
7/1 ⁹	9:25	33.5	5	13	12	9	4	5	43
7/2 ¹⁰	2:27	36.0	4	30	6	0	0	—	36
7/4 ¹¹	11:52	34.0	3	67	0	0	—	—	67

Calculations.

Rises per fish hour	Fish rising in groups by percentage of total:					Minutes without rises in percent ¹³	
	1	2	3	4	5	All	Per fish
16.2	38	28	18	10	06	43	8.6
8.6	67	19	14	00	00	50	10.0
10.6	47	30	23	00	00	46	9.2
10.6	47	30	23	00	00	51	10.2
14.8	68	22	04	00	06	31	6.2
9.4	72	13	06	09	00	50	10.0
10.8	37	33	22	08	00	53	10.6
8.6	30	28	21	09	12	66	13.2
Mean ¹²							
11.2	52	25	16	04	03	49	9.8
9.0	83	17	00	00	—	60	15.0
22.3	100	00	00	—	—	30	10.0

¹ This pool, actually an old alligator hole, which had been artificially enlarged two years previous, is connected with the sea by a cut channel and receives sea water only at the highest spring tides. This channel is choked with fallen palmetto leaves, effectively preventing the passage of even small fish. The pool is usually sufficiently fresh for the island fauna to use for drinking purposes. These include various birds, coons and gopher tortoises. See Table X for analysis of this water. *Gambusia*, *Mollinnesia*, *Cyprinodon* and both fiddler and blue crabs make up the remainder of the aquatic fauna.

² Clear and sunny. Water turbid; reddish colored. The fish used in this experiment measured 48.89, 31.16, 33.02, 30.48, 29.21 cm. in standard length. The first two were removed in the order listed and had been placed in pool March 26, 1939, not having been disturbed since then.

³ Sky overcast, distant thunder. Pool covered with scum of algae, forming bright green bubbles wherever tarpon rolled. Fishes rising very quietly.

⁴ Rain most of previous night. Green scum on pool much reduced. Water much clearer.

⁵ Clear, shadows of palmettos reaching pool. Algal scum forming again. Fish scattered out all over pool. Formerly in deepest part.

⁶ Light clouds passing over sun. Scum no longer green; grayish-brown. A little rain previous night. Tarpon rolling all over pool.

⁷ Clear. Surface of pool cleaner. Tarpon making vigorous splashes.

⁸ Clear. Surface still cleaner. Fish roll well but lazily.

⁹ Clear. Scum as day before.

¹⁰ Clear. Scum completely gone from pool. Day before fish had been caught and measured. One died. Rain in the morning. Fish rising in all parts of pool.

¹¹ Clear. Spring tides. Day before, after the observation period, salt water entered and as this observation was being made water was again running in. Some slight scum on water. Another fish died. Fish feeding vigorously all around edge. Rain previous night. Pool overflowing banks in places. Fish widely scattered.

¹² The preceding footnotes indicate why, with the changed conditions, the last two periods have been omitted from some of the calculations.

¹³ Based on initial data, not shown in first part of table.

TABLE VIII.
Temperature and Rises in Pools.
Calculations Based on Tables VI and VII.

Behavior	Temperature in 5° intervals centigrade				
	16-20	21-25	26-30	31-35	36-40
	0.8	6.0	3.3	16.2	10.6
		10.4	5.1	10.6	9.4
		1.6	8.6	14.8	10.8
Rises per fish hour		2.0		8.6	9.0
		6.0		22.3	
		3.2			
		5.2			
		4.0			
Mean	0.8	4.8	5.7	14.5	10.0
Maximum	0.8	10.4	9.6	22.3	10.8
Minimum	0.8	1.6	3.3	8.6	9.0
	19.6	14.6	7.0	8.6	10.2
		11.4	5.9	9.2	6.2
		18.6	10.0	10.0	10.6
		16.6		13.2	15.0
% minutes without rises, per fish		14.6		10.0	
		16.6			
		14.0			
		14.0			
Mean	19.6	15.0	7.6	10.2	10.5
Maximum	19.6	18.6	10.0	13.2	15.0
Minimum	19.6	14.0	5.9	8.6	6.2
		6:46	3:10	2:61	4:31
		4:57	3:16	2:40	4:18
Greatest unit of time between rises in minutes and seconds ¹		19:18	6:03	3:43	3:23
		8:33	6:05	3:22	5:14
		5:08		2:57	5:02
		8:18		2:05	3:41
		7:26		5:09	4:20
		5:07		5:34	4:01
				3:16	
				2:44	
Mean of all		8:07	4:09	3:43	4:04
Maximum		19:18	6:05	5:34	5:14
Minimum		4:57	3:10	2:05	3:23
Mean (5 fish only)		8:07	3:13	3:04	4:01
Maximum		19:18	3:16	5:34	5:14
Minimum		4:57	3:10	2:05	3:41

¹ In this tabulation, the hour periods of the brackish water pool have been divided in two and read as recorded. All entries refer to groups of five fish except those in italics. From left to right these groups are of 9, 3 and 4 fish respectively.

TABLE IX.

Comparison of "Imitation" in Various-sized Groups and in Various-sized Volumes of Water.

Number of fishes in groups Total time of observation (in hours)	Aquaria		N. J. Pool		Florida Pool		
	2	4	5	9	3	4	5
	36	36	4½	1	1	1	8
No. fish in group rising	No. of rising fish in percent						
1	63	31	58	72	100	83	52
2	37	29	16	22	00	17	25
3	—	25	24	06	00	00	16
4	—	15	02	00	—	00	04
5	—	—	00	00	—	—	03
6	—	—	—	00	—	—	—
7	—	—	—	00	—	—	—
8	—	—	—	00	—	—	—
9	—	—	—	00	—	—	—
	Aquaria		N. J. Pool		Florida Pool		
Area in sq. meters	0.196		15		115		
Volume H ₂ O in liters	48		4,300		70,000		
% of rises alone (weighted means)	47		61		60		
% of group rises (weighted means)	53		39		40		

TABLE X.

Chemical Analysis of Pools in New Jersey and Florida.

Date (1940)	Florida		New Jersey
	June 30	July 4	Aug. 28
Albuminoid ammonia (p.p.m. Nitrogen)	14.000	11.000	.200
Free Ammonia (p.p.m. Nitrogen)	21.000	15.000	.220
Nitrate (p.p.m. Nitrogen)	.25	.25	.25
Chlorine (p.p.m.)	17,400.	18,250.	3.6
Hardness (p.p.m. Calcium carbonate)	8,100	8,100	92
Alkalinity (p.p.m. Calcium carbonate)	106	116	78
PO ₄ (p.p.m.)	1.2	1.7	—
SO ₄ (p.p.m.)	1900	2010	16
Iron (p.p.m.)	.05	.10	.30
Turbidity	1	2	1
Color (p.p.m. Platinum)	220	200	10
Total solids (p.p.m.)	55430	46770	252

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EXPLANATION OF THE PLATES.

PLATE I.

Respiratory behavior of tarpon under varying conditions. See text for explanation.

- Fig. 1. A typical rise through a clean water surface. July 4, 1940.
Fig. 2. A typical rise through an algae-covered surface to left of center. June 26, 1940.
Fig. 3. Two sets of paired respiratory bubbles left entrained on algae-covered surface in lower left. June 25, 1940.

PLATE II.

- Fig. 4. Two tarpon rises at less than a second's interval. The first is represented by the rings of large diameter. Bubbles may be seen at its center from the fish which has already descended. The second, left of center, has not as yet started the Newton's ring formation. Drops are still falling from the splash formed as the fish broke the surface.